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TEMPERATURE AND OXYGEN CONSUMPTION OF ORCHOMONELLA CHILENSIS (HELLER) (AMPHIPODA: GAMMEROIDEA)

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O. chilensis was collected by several antarctic expeditions and probably is antarctic circumpolar (Shoemaker, 1945). The species has previously been divided into several forms or into several separate species; the antarctic populations were named *Orchomenopsis rossi* A. O. W. (Walker, 1903). Chilton (1912) concluded that *Orchomonella chilensis* is a widely distributed and variable species. It was originally described from Chile and has been collected from both the North and South Atlantic Oceans.

Walker (1907) reported *O. chilensis* was present in McMurdo Sound in enormous numbers from May through October and disappeared from the traps between October 25 and January 27, the time of the antarctic summer. However, the animals were readily collected in traps baited with seal meat and placed at a depth of 240 m. off Cape Armitage during the antarctic summer of December, 1960, and January, 1961.

Walker (1907) reported that this amphipod could exist only in water a little above freezing. Because of the recent studies of metabolic compensation in poikilothermic animals, it seemed of interest to measure the relationship between temperature and oxygen consumption of an animal that lives the entire year at a temperature near $-1.8°$ C.

MATERIALS AND METHODS

Animals collected from traps were returned to the laboratory in sea water in insulated cans. The animals were kept in aerated sea water in a constant temperature cabinet at $-1.8°$ C. About 24–48 hours prior to a run, the animals were placed in a refrigerator or water bath at the same temperature as that of the run.

However, because of the lack of facilities for temperature control, the animals were subjected to considerable variation in temperature at temperatures exceeding 2° C.

Wide-mouth bottles of about 60 cc. capacity were used as respirometers. Fresh, filtered sea water was aerated for 12 hours prior to a run. Sufficient water was stirred in a large beaker to fill 24 bottles. Three bottles were used as controls and one animal was placed in each of the remaining 21 bottles. All bottles were closed with a glass stopper and checked for air bubbles. The bottles were placed in a rack and the rack placed in a covered water bath of the proper temperature. Temperature of the water bath varied about 0.1° C. Most runs were 4 hours, but some were 6 or 8 hours.

At the end of each run, the amount of dissolved oxygen in each bottle was determined by means of the unmodified Winkler method. The difference between the amount of oxygen in a bottle with an animal and the mean of the three controls

TABLE I

Oxygen consumption and body size of Orchomonella chilensis (Heller)

Tempera-ture, ° C.	Mean wet weight, nearest mg.	Oxygen consumption (µl./gm./hr.)		Coefficients					
				$O_2:W$			$\dfrac{O_2:W}{W}$		
		$\bar{x}$	S.E.$\bar{x}$	b	S.E.$_b$	r^{**}	$b-1$	S.E.$_{b-1}$	r^{**}
−1.8	67	128.3	0.17	0.455	0.103	0.408	−0.470	0.093	−0.455
0	87	117.7	0.15	0.471	0.058	0.631	−0.530	0.059	−0.675
2	86	141.2	0.16	0.462	0.106	0.403	−0.467	0.091	−0.459
4	75	124.3	0.16	0.665	0.083	0.630	−0.353	0.099	−0.339
6	71	146.8	0.17	0.642	0.107	0.519	−0.309	0.108	−0.278
8	71	158.8	0.14	0.604	0.061	0.707	−0.393	0.061	−0.543
10	70	231.0	0.10	0.571	0.078	0.596	−0.448	0.062	−0.590
12	75	176.8	0.15	0.497	0.069	0.587	−0.589	0.090	−0.553

All values of r highly significant. Test for heterogeneity of r: null hypothesis, all r's are from the same population. For $O_2:W$, $\chi^2 = 16.92$, d.f. $= 7$, $.02 > P > .01$. Reject null hypothesis. $\dfrac{O_2:W}{W}$, $\chi^2 = 20.57$, d.f. $= 7$, $.01 > P > .001$. Reject null hypothesis.

was the amount of oxygen used. Each animal was blotted dry and its wet weight determined on a Mettler Type B5 analytical balance. Because no brooding female amphipods were found, the sex of the animals was not determined.

A preliminary survival experiment indicated that the animals were intolerant to temperatures above 15° C. Therefore, runs were made at −1.8° C., 0° C. and at 2° intervals through 12° C. At 12° C., there was considerable mortality in the respirometers and it was not feasible to make determinations of oxygen consumption at higher temperatures. The oxygen consumption of 100 animals was determined at each temperature; 800 animals were used overall.

Two sources of error should be noted. No attempt was made to control activity. There was no control over the amount of feeding by the animals except they had not fed for at least 24 hours prior to being used. In addition, the animals were not acclimated to the experimental temperatures. Thus the R-T curve is acutely

measured. Probably the animals lived for several months at $-1.8°$ C. or slightly warmer before they were brought into the laboratory.

OXYGEN CONSUMPTION AND SIZE

The consumption of oxygen per unit time is a function of size as expressed in the following equation:

$$(1) \quad O_2 = aW^b,$$

where W = weight and a and b are constants. Equation (1) may be divided by W to produce a weight-specific respiration:

$$(2) \quad \frac{O_2}{W} = aW^{b-1}.$$

In these equations, b and $b-1$ are regression coefficients. For crustaceans, b is generally between 0.67 and 1.0 and $b-1$ is usually between -0.05 and -0.40 (Wolvekamp and Waterman, 1960).

The regression coefficients of double-logarithmic plots were determined by the method of least squares. Additional statistics calculated were the standard errors of b and $b-1$ and the coefficients of correlation (r) (Table I). A different b (Fig. 1) or $b-1$ was obtained at each temperature. Because the standard errors were so variable, the regression lines of b were tested for homogeneity by an analysis of covariance (Steel and Torrie, 1960; p. 319). The null hypothesis, there is no difference in regression coefficients for log oxygen consumption against log weight at the 8 temperatures, was tested by means of the F test. Because $F = 5.407$ ($p<.01$), the null hypothesis was rejected and it was concluded that the regression lines were different from one another. However, there was considerable heterogeneity in the unexplained SS at 8°, 10° and 12° C. Therefore, a second test for homogeneity was made, omitting the three higher temperatures. Because $F = 5.66$ ($p<.01$), it was concluded that the regression slopes were heterogeneous.

Heterogeneity in regression slopes was found in *Artemia salina* (Conover, 1960), in the snails *Lymnaea palustris* and *L. pereger* (Berg and Ockelmann, 1959) and in the crabs *Uca pugnax* and *U. rapax* (Vernberg, 1959). Vernberg and Conover demonstrated a direct effect of temperature on b or $b-1$. Berg and Ockelmann demonstrated a seasonal shift in b; when the animals were tested at 18° C., the slope of the regression line was greater in June than in August. The authors suggested that the seasonal variation might be caused by a comparatively greater increase of oxygen consumption by the larger animals during the season of reproduction. However, in this regard, Rao and Bullock (1954) showed that habitat temperature of the animal prior to study could affect Q_{10} and that Q_{10} commonly increases with increasing size over the range of normal physiological activity. Presumably the differences in habitat temperatures might account for the differences reported by Berg and Ockelmann, although it is not unlikely that several interacting factors were present.

Temperature seems more likely to be the primary factor in explaining the variation of b in *O. chilensis*. The animals were collected from an environmental temperature that probably varied less than 1° C. for several months, nor were the animals reproducing. Although Q_{10} was not calculated, it is evident from Figure 2
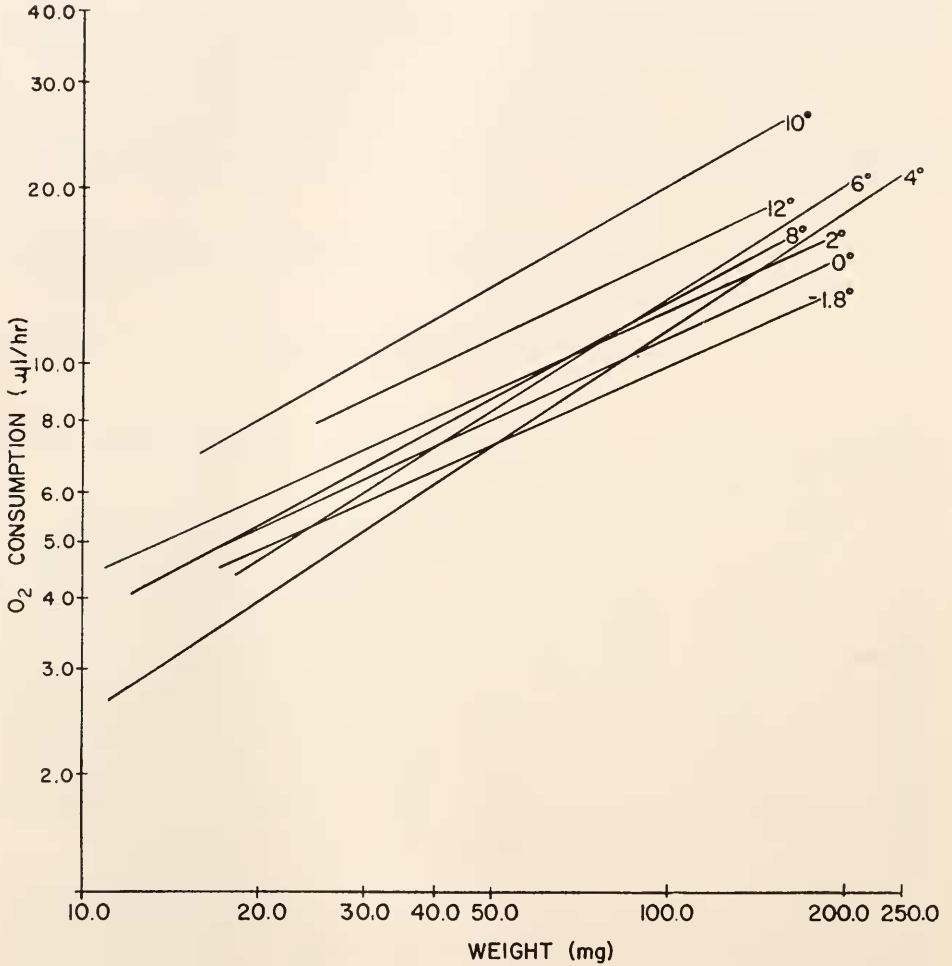
Figure 1. The relationship between oxygen consumption and body size in *Orchomonella chilensis* (Heller). Temperature is degrees Celsius (C).

that Q_{10} varied with size. Small animals greatly reduced oxygen consumption at 4° C. as compared with 2° C. With increasing size, the amount of reduction decreased and the largest animals increased consumption. Another trend appeared between 6° and 8°, the smallest animals increasing and the largest animals decreasing consumption.

These trends are supported by the values of r. Because the distribution of r's is asymmetrical, all r's were converted to the normally distributed z and the z's tested for homogeneity. The null hypothesis, all r's are from the same population, was rejected (Table I). Therefore, it is evident that the relationship, $O_2:W$, is influenced by temperature. The z's were tested for significant differences (Table II). Significant differences, among others, occurred between 2° and 4° C. and
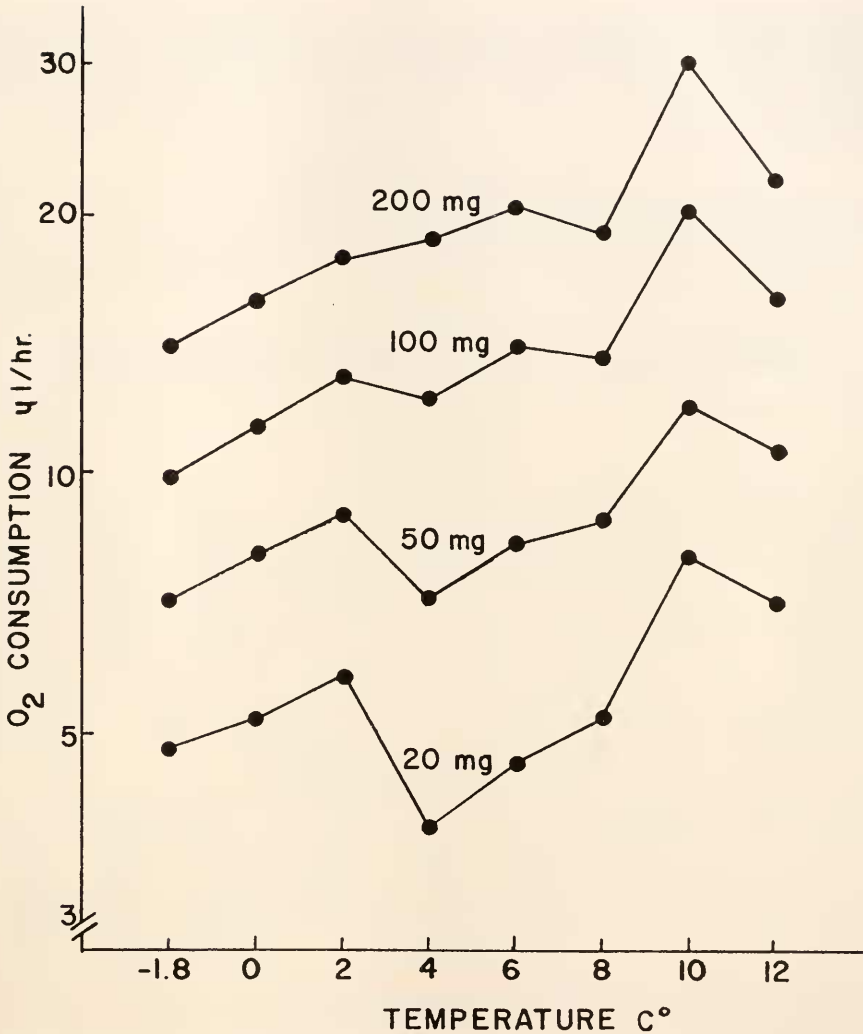
FIGURE 2. The relationship between oxygen consumption and temperature for different sized *Orchomonella chilensis* (Heller).

between 6° and 8° C. Similar results were obtained comparing the r's of the relationship $O_2/W:W$. However, the distribution of significant differences among z's of the weight-specific rate:weight values differed from the distribution of significant differences among z's of the rate:weight values. Although the general conclusion that temperature affects the rate:weight relationship does not depend on the method of evaluating rate, the specific effects of temperature do depend on the method of analysis.

According to von Bertalanffy and Krywienczyk (1953), if $b = 0.66$, metabolism is proportional to surface; if $b = 1.0$, metabolism is proportional to weight; if

$^b > 0.66$, but < 1.0, metabolism is intermediate. The values of ^{b} for *O. chilensis* indicate several metabolic types in the population including types not included in the above scheme. Locker (1961), however, believes that metabolism is basically related to surface, but this relationship can be modified by factors such as temperature.

RATE-TEMPERATURE CURVE

The shape of the R-T curve (Fig. 3) will depend, in part, on the size of the animals used and will reflect the composition of the population at the time the

TABLE II

Differences between r's converted to z. All differences exceeding the LSD marked with an asterisk

°C.	−1.8	0	2	4	6	8	10	12
				Rate:Weight (O_2:W)				
−1.8	0	.310*	.006	.308*	.142	.448*	.254	.240
0		0	.316*	.002	.168	.138	.056	.070
2			0	.314*	.148	.454*	.260	.246
4				0	.167	.140	.055	.068
6					0	.306*	.112	.098
8						0	.194	.208
10							0	.014
12								0
				Weight-specific Rate:Weight $\frac{(O_2:W)}{W}$				
−1.8	0	.329*	.005	.137	.206	.117	.187	.131
0		0	.324*	.466*	.534*	.212	.142	.198
2			0	.142	.211	.112	.182	.126
4				0	.069	.254	.324*	.268
6					0	.323*	.392*	.336*
8						0	.069	.013
10							0	.056
12								0

Significant differences among z's: $t = z_1 - z_2 \Big/ \sqrt{\dfrac{2}{n-3}}, = 0.282$.

animals were collected. For example, oxygen consumption was higher at 0° C. than at −1.8° C. for each size class (Fig. 2), but the rate at 0° C. was lower than at −1.8° C. (Fig. 3) because the population at −1.8° C. averaged 20 mg. less in size (Table I). However, the decrease of oxygen consumption at 4° C. occurred in all except the largest members of the population (which were rare) and therefore seems characteristic of the population in general. This decrease appears to be an adaptation to high temperatures. The adaptation lies in the vertical displacement of the R-T curve and suggests a change in Q_{10}. This change might be brought about by a shift in the control of metabolic reactions to an alternate enzymatic pathway.

Following the shift between 2° and 4° C., the rate of oxygen consumption increased and beyond 8° metabolic control was inadequate. Under acclimated conditions, the animals might be fairly good regulators to 6° or 8° C., but would likely be conformers in any event at temperatures above 8° C. One might not expect such a high degree of regulation in a species living at such a narrow range of environmental temperature. It would be interesting to determine the response pattern of the species in other parts of its geographical range, as the R-T curve of the antarctic population may result from the genetic history of populations that previously lived in waters with wider fluctuations of temperature than now seem to occur in McMurdo Sound.

The levels of oxygen consumption were about the same as arctic amphipods (Scholander *et al.*, 1953) and were higher than in amphipods of temperate regions (Wolvekamp and Waterman, 1960), when the differences in experimental tem-
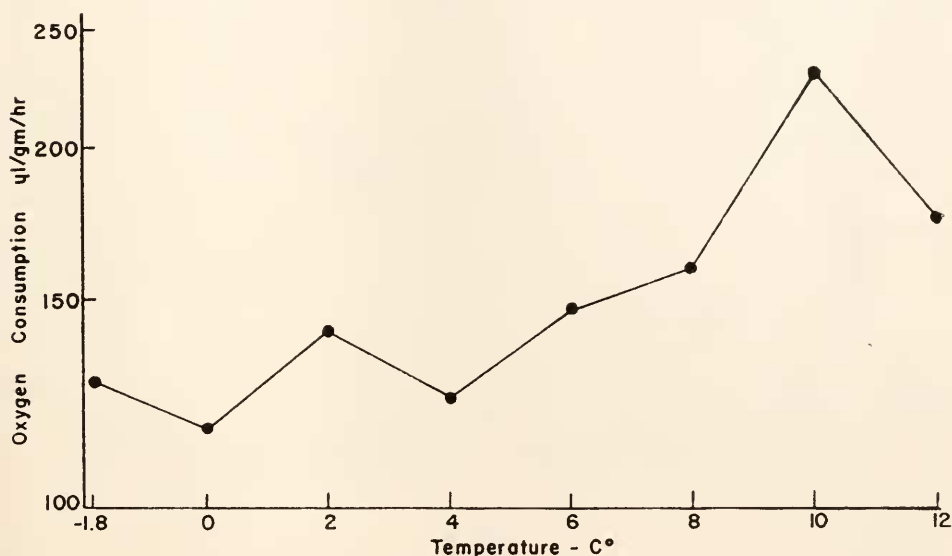

FIGURE 3. The acutely determined R-T curve for populations of
Orchomonella chilensis (Heller).

peratures are eliminated by extrapolating the curves of temperate species downward or projecting the slope between 8° and 10° of *O. chilensis* upward. Thus, *O. chilensis* clearly demonstrates metabolic compensation (Bullock, 1955).

SUMMARY

1. The rate of oxygen consumption of the antarctic amphipod *Orchomonella chilensis* (Heller) was determined over a graded temperature series from −1.8° to 12° C.

2. The regression coefficients of double-log plots of rate:weight and weight-specific rate:weight were temperature-dependent. The correlation coefficients

between size and rates of consumption were highly significant and varied significantly with temperature. Q_{10} varied with size.

3. The acutely determined R-T curve shows some regulation between $-1.8°$ and $6° C$. Metabolic compensation was evident.

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